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Dive behaviour can predict metabolic expenditure in Steller sea lions

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Quantification of costs associated with foraging contributes to understanding the energetic impact that changes in prey availability have on the energy balance of an animal and the fitness of populations. However, estimating the costs of foraging is difficult for breath-hold divers, such as Steller sea lions, that feed underwater. We developed models parameterized with data from free-diving captive Steller sea lions to estimate the costs incurred by wild animals while foraging. We measured diving metabolic rate of trained sea lions performing four types of dives to 10 and 40 m in the open ocean and estimated the separate costs of different dive components: surface time; bottom time; and transiting to and from depth. We found that the sea lions' diving metabolic rates were higher while transiting (20.5 ± 13.0 ml O_2 min^{-1} kg^{-1}) than while swimming at depth (13.5 ± 4.1 ml O_2 min^{-1} kg^{-1}), and both were higher than metabolism at the surface (9.2 ± 1.6 ml O_2 min^{-1} kg^{-1}). These values were incorporated into an energetic model that accurately predicted oxygen consumption for dives only (within 9.5%) and dive cycles (within 7.7%), although it consistently overestimated costs by 5.9% for dives and 21.8% for dive cycles. Differences in the costs of individual components of dives also explained differences in the efficiency of different dive strategies. Single dives were energetically less costly than bout dives; however, sea lions were more efficient at replenishing oxygen stores after bout dives and could therefore spend a greater portion of their time foraging than when undertaking single dives. The metabolic rates we measured for the different behavioural components of diving can be applied to time–depth recordings from wild Steller sea lions to estimate the energy expended while foraging. In turn, this can be used to understand how changes in prey availability affect energy balance and the health of individuals in declining populations.

Key words: Diving metabolic rate, foraging energetics, Steller sea lion

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Introduction

The ability to determine accurately the costs of underwater activity for breath-hold divers is essential for understanding the energetics of diving and associated foraging strategies. Foraging is one of the largest components of an animal's energy budget and has major impacts on overall energy balance. Accurate estimates of diving costs are needed to understand how physiological constraints and energetic demands may affect foraging costs and strategies in the wild in different environmental conditions.

Steller sea lion (*Eumetopias jubatus*) populations in Alaska have declined by ~80% since the 1970s, possibly because of changes in prey availability, abundance or nutritional quality (Loughlin *et al.*, 1998; Trites and Donnelly, 2003). Any of these factors could, in theory, affect foraging behaviour, the

associated foraging costs, and thus, the animal's overall energy balance. Several studies have examined how reductions in the quantity or quality of food affect the physiology of Steller sea lions (Rosen *et al.*, 2000; Rosen and Trites, 2000, 2004; Atkinson *et al.*, 2008; Jeanniard du Dot *et al.*, 2009; Gerlinsky *et al.*, 2014); however, few studies have looked at how foraging costs may be affected by reductions in the quantity and quality of prey.

Optimal foraging models for breath-hold divers suggest that animals should maximize their energetic efficiency by altering their dive behaviours in response to the depth and abundance of prey (Houston and Carbone, 1992; Carbone and Houston, 1996; Thompson and Fedak, 2001). Previous studies with captive Steller sea lions, as well as with other pinniped species, have shown that animals do change their dive behaviour in response to changes in prey location and abundance (Cornick and Horning, 2003; Sparling *et al.*, 2007) and that these behavioural modifications can negatively impact foraging costs and overall foraging efficiency (Goundie *et al.*, 2015). However, testing these model predictions on declining wild populations based on the results of captive studies requires a reliable means to quantify energetic expenditure during diving in free-ranging animals. An ability to quantify the costs of different diving behaviours would also permit the costs and benefits of different diving strategies to be compared.

Respirometry—the direct measurement of O_2 consumption and CO_2 production—is the most accurate method available to measure metabolic costs of diving. It works over both fine- and long-term time scales (Boyd, 2002; Fahlman *et al.*, 2008b) but is challenging when dealing with wild diving animals (Boyd, 2002) and is generally not plausible with marine mammals, except with animals that reliably resurface within ice holes (Kooyman *et al.*, 1973). The doubly labelled water dilution method is often used in field studies to estimate CO_2 production in relationship to diving behaviour (Boyd *et al.*, 1995b; Sparling *et al.*, 2008; Dalton *et al.*, 2014). However, because of the relatively large time scale associated with this technique, it is difficult to quantify the costs of different, specific activities.

Other methods have been tested as proxies for direct measurements of diving metabolic rate and have shown varying levels of success when compared with direct measurements. Heart rate can predict energy expenditure in certain conditions, but it is complicated by the cardiovascular adjustments that take place in diving animals, requires separate predictive equations for different activities and often requires the use of invasive tags (McPhee *et al.*, 2003; Hindle *et al.*, 2010; Young *et al.*, 2011). Overall dynamic body acceleration measures three-dimensional body acceleration that should, in theory, correspond to energy expenditure (Wilson *et al.*, 2006). Although some studies demonstrate solid relationships between overall dynamic body acceleration and energy expenditure in some species of diving animals (Fahlman *et al.*, 2008c, 2013; Enstipp *et al.*, 2011; Halsey *et al.*, 2011a), others indicate that this relationship does not hold for all activities (Halsey *et al.*, 2011c; Dalton *et al.*, 2014; Volpov *et al.*, 2015). There is also evidence that the relationship between overall dynamic body acceleration and metabolic rate may be impacted by body mass, drag, buoyancy and swimming strategies (King *et al.*, 2004; Gleiss *et al.*, 2011; Halsey *et al.*, 2011b,c). Flipper stroke rate has been shown to provide a reliable measure of instantaneous effort and energetic output in some species (Williams *et al.*, 2004; Insley *et al.*, 2008; Maresh *et al.*, 2014). This method is useful because it is able to account for specific types of swimming and diving activities (i.e. gliding vs. active propulsion) to provide a clearer picture of effort. However, this method may be less precise for Steller sea lions (Hindle *et al.*, 2010). Similar to overall dynamic body acceleration, stroke rate may not be able to account for the physiological adjustments that occur during diving and digestion.

While these different high-tech, data-intensive techniques show various levels of promise, a more simple method estimates energetic expenditure during foraging through activity budgets (Boyd *et al.*, 2010). Behavioural time budgets are coupled with estimates of activity-specific rates of energy expenditure, generally derived from captive studies or are simple multipliers of an estimated resting metabolic rate. Both the proportion of time spent diving and the specific dive characteristics are relatively easy to obtain from wild animals equipped with time–depth recorders (TDRs). However, most studies using this method apply only a single overall energetic cost to all diving activity (Costa *et al.*, 1989; Winship *et al.*, 2002), which inherently assumes an equivalent and constant cost of diving. In contrast to this assumption, pinnipeds generally perform a variety of dive behaviours related to different dive types (Schreer *et al.*, 2001; Thums *et al.*, 2008) that are likely to have different costs. Hence, this technique is unable to determine the impact of changes in foraging behaviour independent of gross changes in overall dive time.

The metabolic costs of different types of diving behaviour, such as the costs of diving at different depths and with varying levels of activity, have been measured in captive Steller sea lions (Hastie *et al.*, 2006a,b; Fahlman *et al.*, 2008b,c; Gerlinsky *et al.*, 2013). However, these previous studies quantified only the total metabolic cost over the entire dive or dive series. While these experimental manipulations of dive types (i.e. depth, activity level and submergence time) have provided insights into the effects of different diving strategies and behaviours on energetic costs, the specific contributions of different phases of the dive to total costs have been impossible to discern. This makes it difficult to estimate the energetic costs of different dives and extrapolate the results into more generalized models of diving bioenergetics and associated foraging strategies that can be applied to the wider variety of dive behaviours seen in wild animals.

Our study separated and measured the costs of individual components of dives in trained Steller sea lions diving in the open ocean. Our goal was to use measurements of diving costs and behaviours in free-diving captive sea lions to develop a model to estimate the diving costs of wild Steller sea lions

from readily available TDR data and to model the energetic impacts of different dive types. This would provide a new tool to estimate energy expenditure of diving Steller sea lions using only time–depth recorders. Not only are these tags readily available, minimally invasive, inexpensive and easy to use, but they have also been regularly deployed on animals for decades. This creates the opportunity to look back into historical dive data and compare foraging costs during different phases of the population decline.

We also wanted to compare and understand the root differences in the efficiency of different dive strategies. This would allow the costs and benefits associated with various foraging strategies to be assessed and would provide insight into how changing foraging strategies resulting from changes in prey availability may impact the foraging costs and overall energy balance of wild Steller sea lions. The ability to estimate diving costs accurately and to assess foraging strategies, both historical and current, may be able to provide valuable insight into whether or not altered foraging costs may have contributed to the decline of Steller sea lions.

Materials and methods

Data collection

We measured diving metabolic rates (DMRs) of four adult female Steller sea lions performing specific dive patterns and separated the costs associated with different parts of a dive. Specifically, we targeted the costs of resting at the surface, transiting to and from depth, and the effect of different levels of foraging activity at depth. Data were collected between February and May 2013 from two 13-year-old and two 16-year-old sea lions, weighing between 150 and 229 kg. All animals were wild-born and raised at the Vancouver Aquarium (Vancouver, BC, Canada). The sea lions were housed at the University of British Columbia's Open Water Research Station (Port Moody, BC, Canada) for 4–8 years, and had previously been trained to be familiar with all experimental equipment and to perform dive trials in the open ocean voluntarily under trainer control. Experiments were conducted under UBC Animal Care Permit #A11-0397.

Metabolic rates

We measured rates of oxygen consumption via flow-through gas respirometry (as described by Goundie *et al.*, 2015), with the sea lions performing a variety of pre-set dive types described below. In brief, we measured metabolic rate in a 100 l Plexiglass dome floating on the surface of the water. Air was drawn through the dome at a rate of 475 l min^{-1} and was sub-sampled and scrubbed of water vapour via $CaSO_4$. Concentrations of oxygen and carbon dioxide in the incurrent and excurrent flows were measured using Sable System FC-1B and CA-1B analysers, coupled to a 500H mass flow generator and controller (Sable Systems, Las Vegas, NV, USA) and recorded every 0.5 s to a PC (Sable Data Acquisition System, Sable Systems Inc.). Metabolic data were analysed using LabAnalyst X (Warthog Systems, Mark Chappell, University of California) and oxygen consumption rates were calculated using eq. 3b in the study by Withers (1977).

We measured pre-dive metabolic rate (MR_S) while animals rested calmly at the surface in the metabolic dome before each dive trial. The MR_S was calculated as the average rate of oxygen consumption during the last 2 min of a 5–10 min period when oxygen concentrations were stable. Post-dive rates of oxygen consumption were measured to calculate oxygen consumed during the dive and to determine dive recovery time (i.e. the amount of time at the surface needed for oxygen consumption to return to within 5% of MR_S).

We calculated diving metabolic rate (DMR) as the total volume of oxygen consumed above resting levels at the surface (MR_S), divided by the dive duration (submergence time). This provided an estimate of the metabolic expenditure for only the submerged portion of the dive and excluded the time and energy spent at the surface. Differences in DMR during dives with different characteristics (see below) allowed us to calculate the costs associated with individual components of a dive.

Trial protocol

The sea lions were trained to dive voluntarily between the metabolic dome at the surface and the end of either one or two feeding tubes set at depths of either 10 or 40 m. These depths are representative of dive depths observed in wild Steller sea lions (Merrick and Loughlin, 1997). During dives, 0.02 kg pieces of Pacific herring (*Culpea pallasii*) were delivered to the sea lions at depth via the feeding tubes at a rate of 12 pieces per minute. Depending on trial protocols, fish pieces were either pumped alternately out of each feeding tube to encourage movement between the tubes or pumped out of a single tube so that the animals would remain fairly stationary at depth.

Animals were fasted overnight before trials and transported to the dive site by boat. During transport and measurements of pre-dive MR_S, the sea lions received minimal food reinforcement (<0.8 kg) to reduce the potential impact of digestion on metabolic rate. Given previous measurements of the time course of digestion in non-diving sea lions, the fact that the trials were only ~1 h long, and previous studies demonstrating that Steller sea lions partly defer digestion while diving, it is unlikely that the heat increment of feeding influenced our results (Rosen and Trites, 1997; Rosen *et al.*, 2015). Our sea lions performed four different dive types at each depth (Fig. 1), and all animals completed three trials of each dive type and depth combination for a total of 96 dive trials. Animals completed one to three trials per session and had a minimum of 1 day off between trials. The dive types were as follows.

(i) Transit dives were single dives where animals dived to depth and back to the surface with no bottom time.

(ii) Stationary dives were single dives where animals dived to depth and remained stationary at one feeding tube for 3 min of bottom time.

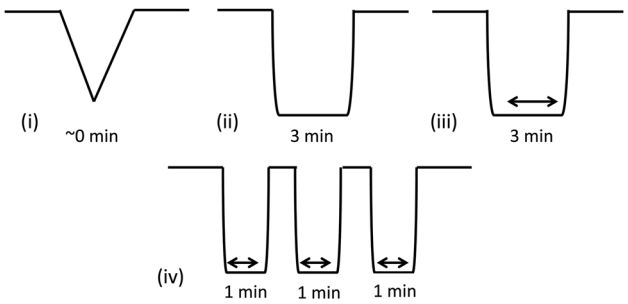

Figure 1: Schematic diagram illustrating experimental dive types, showing changes in depth over time (not distance). For transit dives (i), the Steller sea lions dived to depth and immediately returned to the surface with little to no bottom time. Stationary dives (ii) included 3 min of non-active bottom time at one feeding tube. Active dives (iii) included 3 min of active bottom time spent swimming between two feeding tubes. Bout dives (iv) consisted of three consecutive dives with 1 min of active bottom time each. Each animal completed three trials for each dive type at 10 and 40 m.

(iii) Active dives were single dives where animals dived to depth and travelled between the two feeding tubes for 3 min of bottom time.

(iv) Active bouts were bouts of three consecutive dives, each with 1 min of bottom time (for a total of 3 min to be comparable to the single active dives that also had a total of 3 min of bottom time). Inter-dive surface intervals were set at ~20 s for 10 m dives and ~35 s for 40 m dives (the sea lions received <0.2 kg during each inter-dive surface interval). Surface interval times for these bouts were chosen as the shortest time possible to ensure that the sea lions did not recover fully between dives, but where animals would reliably continue diving. Minimizing inter-dive surface intervals differentiated between single and bout dives. Without a full recovery between dives, dive bouts were considered a single physiological event (yielding a single average DMR estimate). This allowed us to compare total dive costs and recovery times for dive bouts with the single dives.

Specific bottom durations for these dive types were achieved by turning off a light at the bottom of the feeding tubes (animals were previously trained to return to the surface once the light was turned off). Each animal was outfitted with a tight-fitting harness holding a time–depth recorder (ReefNet, Inc., Mississauga, ON, Canada) to record dive behaviour and confirm bottom times.

Calculating separate dive components

The cost of transit ($DMR_{Transit}$) to and from 40 m depth was measured directly as the DMR for the transit dives. However, DMR for transit dives to 10 m could not be measured directly, as they were only ~15 s long, which was insufficient to register an increase in oxygen consumption reliably after a dive. Hence, the rate of oxygen consumption for 10 m transit dives was extrapolated from the DMR measured for 40 m transit dives and the dive duration for the 10 m dives. This assumed similar metabolic rates for transiting to different depths. This is likely to be the case, because previous studies have indicated that any metabolic adjustments associated with dive depth do not occur immediately, indicating that metabolic rates should be similar for the beginning portions of the dives to both depths (Hindle *et al.*, 2010).

We calculated the cost associated with the bottom portion of a dive (DMR_{Bottom}) for the stationary and active single dives as follows:

$$DMR_{Bottom} = \frac{(O_2\,consumed_{Total} - O_2\,consumed_{Transit})}{Bottom\,time} \quad (1)$$

This provides DMR for the specific type of bottom activity only. Separate averaged values for $DMR_{Transit}$ for each animal were used in this calculation. All times for transit and the bottom portions of the dives were extracted from the TDR data.

Validation

To test whether the estimates of DMR that we calculated from the individual components (surface, transit and activity-specific bottom times) could be used to predict total diving cost for other, more complex dives, we compared calculated volumes of oxygen consumption (using the DMR estimates of each dive component) with the measurements of oxygen consumption for an independent set of dives from a previous study with the same general experimental set-up and animals (Goundie *et al.*, 2015). For these trials, rates of oxygen consumption were measured over bouts of five consecutive dives of varying duration, where the sea lions chose both dive duration and inter-dive surface interval. Predicted rates of oxygen consumption were estimated using associated TDR data that provided the transit, bottom and surface times for each dive.

Total volume of oxygen consumed was calculated separately for 'dive only' ($\dot{V}_{O_2dive}$) and for a complete 'dive cycle' ($\dot{V}_{O_2cycle}$). The $\dot{V}_{O_2dive}$ estimates solely the oxygen consumed during the portion of the dive cycle spent underwater (i.e. actively diving), whereas $\dot{V}_{O_2cycle}$ refers to the total oxygen consumed during all portions of the entire dive event (i.e. diving, inter-dive surface interval and recovery time). While dive only and dive cycle measurements can be made for both single dives and dive bouts, for the present study we predicted oxygen consumption only for dive bouts.

For the estimates of $\dot{V}_{O_2dive}$, transit and bottom times (T) of those dives were multiplied by the DMR for each respective portion of the dive calculated in the previous phase of the study. This provided separate estimates of oxygen consumed for the transit and bottom portions of the dives, which could be summed to provide an estimate of the total oxygen consumed over the entire submerged portion of the dive, as follows:

$$\dot{V}_{O_2dive} = (T_{Transit} \times DMR_{Transit}) + (T_{Bottom} \times DMR_{Bottom}) \quad (2)$$

For dive cycles (including oxygen consumption both during submergence and at the surface), we calculated the additional oxygen consumption during time spent at the surface (both inter-dive surface intervals and post-dive recovery periods) using estimates of MR_S such that:

$$\dot{V}_{O_2cycle} = (T_{Transit} \times DMR_{Transit}) + (T_{Bottom} \times DMR_{Bottom}) + (T_{Surface} \times MR_S) \quad (3)$$

We then compared both of these estimates of oxygen consumption (equations 2 and 3) with the measured volume of oxygen consumed for the same dives to determine the accuracy of each for estimating diving costs.

Statistical analysis

We used R software (R Core Team, 2014) and linear mixed-effects models (lme) from the nmle package (Pinheiro *et al.*, 2015), with significance set at $\alpha = 0.05$. To account for repeated measures with each animal, models included animal identity as a random effect. Fixed effects were trial depth and either full dive type (single stationary, single active or bout) or dive component (transit, stationary bottom or active bottom). We ran our models using the maximum likelihood method and we used a log likelihood ratio test (LRT) to compare full and reduced models to test the effect of each factor individually and determine the best model to fit the data (Pinheiro and Bates, 2000). Full models included two fixed factors (depth and full dive type or depth and dive component), whereas the reduced models had one factor removed. A significant result indicated that the full model was a better fit to the data and that the factor removed had a significant effect. When dive or component type was a significant factor, we performed *post hoc* analyses with Bonferroni-adjusted *P*-values to determine differences between types by comparing marginal means from mixed-effects models. For single model ANOVA's, *F*- and *P*-values were reported for slopes only, as all intercepts were significantly different from zero.

The first analysis compared the calculated costs of separate dive components. Specifically, the partitioned cost of transit, stationary and active dive components were compared, with depth as an additional potential model component. Next, the total costs (DMR) of both single dive types (stationary and active) and bout dives were compared, again with depth included as a potential model factor. Likewise, the effect of dive type and depth on post-dive recovery time and cumulative recovery time (which includes both post-dive recovery time and inter-dive surface interval times) were tested. The relationship between recovery times and total volumes of oxygen consumed was also tested. Transit dives were not included in these full dive comparisons, as they were designed only for calculating the cost of individual dive components.

We next used a linear mixed effects model (lme) to determine the relationship between the measured and calculated values of oxygen consumption in the additional dive set, and the difference (expressed as a percentage) between the measured and calculated values. Model fits were assessed by separating variance into fixed and random effects. Marginal r^2 values are provided for fixed effects and conditional r^2 values for random effects (Nakagawa and Schielzeth, 2013). To determine whether the slopes for the relationship between the measured and calculated volumes of oxygen consumed were significantly different from 1, we used the slope.test function from the smatr package in R (Warton *et al.*, 2012). Finally, we calculated 95% confidence intervals for the slopes and the average percentage residual.

Oxygen consumption data were tested as both absolute and mass-specific values (i.e. per kilogram). Results did not differ between methods, so we reported mass-specific data to facilitate comparison with other studies. All values are reported as means ± SD.

Results

Diving energetics

Pre-dive surface metabolic rate (MR_S) for all trials ranged from 6.5 to 14.0 ml O_2 min^{-1} kg^{-1} with an average of 9.2 ± 1.6 ml O_2 min^{-1} kg^{-1}. Diving metabolic rate (DMR) was not affected by depth in any of the dive types (LRT = 0.060, $P = 0.81$), so depths were combined for each dive type.

Comparing the DMR of single dives (with and without bottom activity) and bout dives revealed a significant effect of dive type (single or bout) on DMR (LRT = 29.53, $P < 0.0001$). Surprisingly, activity level during the bottom portion of a dive did not affect DMR ($P = 0.35$). The average DMR was 13.8 ± 3.8 ml O_2 min^{-1} kg^{-1} for single stationary dives and 14.9 ± 2.9 ml O_2 min^{-1} kg^{-1} for active dives (Table 1). Bout dives had a higher DMR than single dives ($P < 0.001$), averaging 18.0 ± 2.8 ml O_2 min^{-1} kg^{-1}.

Comparing post-dive recovery times following single and bout dives revealed no effect of depth (LRT = 1.62, $P = 0.20$), dive type (LRT = 2.57, $P = 0.28$) or total oxygen consumption (ANOVA, $F_{1,67} = 3.47$, $P = 0.07$) on recovery time. Recovery times were 6.3 ± 1.5 min for stationary dives, 6.0 ± 1.0 min for active single dives and 5.8 ± 1.2 min for bout dives. In other words, even though bout dives were more costly, recovery time did not increase. This was probably because the sea lions replenished some oxygen at the surface between dives, instead of only during the post-dive recovery period.

Cumulative recovery time (calculated to include both surface intervals and post-dive recovery times, and thereby, to account for the oxygen replenished during inter-dive surface intervals during bout dives) was also not affected by depth (LRT = 3.48, $P = 0.062$) or dive type (LRT = 4.71, $P = 0.095$), owing to the large overlap in dive duration between types. However, cumulative recovery time was significantly related to the total volume of oxygen consumed (ANOVA, $F_{1,67} = 28.77$, $P < 0.0001$; Fig. 2).

Despite the higher DMR and generally larger volumes of oxygen consumption during bout dives, recovery time was still

Table 1: Diving energetics and durations used to calculate the metabolic costs of separate dive components for Steller sea lions performing three different dive types to 10 and 40 m

Dive type	Vol. O_2 full dive (ml kg^{-1})		DMR full dive (ml O_2 min^{-1} kg^{-1})		Dive duration (min)		Transit time (min)		Bottom time (min)		Vol. O_2 component (ml kg^{-1})		DMR component (ml O_2 min^{-1} kg^{-1})	
	10 m	40 m	10 m	40 m	10 m	40 m	10 m	40 m	10 m	40 m	10 m	40 m	10 m	40 m
Transit	4.7 ± 0.3	17.1 ± 11.5	20.5 ± 13.4	20.5 ± 13.4	0.2 ± 0.0	0.9 ± 0.1	0.2 ± 0.0	0.8 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	4.7 ± 0.3	17.1 ± 11.5	20.4 ± 13.2	20.5 ± 13.4
Stationary	43.1 ± 15.7	55.4 ± 11.1	13.3 ± 4.8	14.4 ± 2.6	3.3 ± 0.1	3.8 ± 0.1	0.3 ± 0.0	0.9 ± 0.1	3.0 ± 0.1	2.9 ± 0.1	38.4 ± 15.8	38.2 ± 12.0	12.8 ± 5.1	13.1 ± 4.0
Active	51.6 ± 11.8	54.6 ± 7.6	15.6 ± 3.6	14.3 ± 1.9	3.3 ± 0.1	3.8 ± 0.1	0.3 ± 0.1	0.8 ± 0.1	3.1 ± 0.1	3.0 ± 0.1	46.8 ± 12.1	37.6 ± 8.0	15.4 ± 4.1	12.5 ± 2.4

Dive types included transit dives with no bottom time, stationary dives with 3 min of non-active bottom time and active dives with 3 min of active bottom time (Fig. 1). The volume of oxygen consumed and the diving metabolic rate (DMR) of the separate components were calculated from the total volume of oxygen consumed and the complete dive durations, transit times and bottom times. The DMR of transit to 40 m was measured directly from the transit dives, and the transit costs for 10 m dives were extrapolated from dive times. The DMR of the bottom portion of the dive was calculated by subtracting the volume of oxygen consumed during a transit dive from the total volume consumed during the stationary or active dive types. This was then divided by the bottom time of the dive to obtain the DMR of the bottom portion of the dive. The DMRs of full dives are also included for comparison with components only.

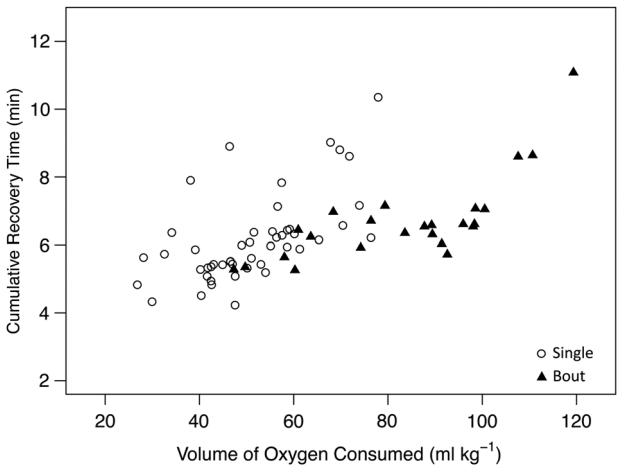

Figure 2: Cumulative recovery time of Steller sea lions as a function of the volume of oxygen consumed during single and bout dives. Cumulative recovery time includes all inter-dive surface intervals and post-dive recovery times. Each point represents a single dive or single dive bout. Open circles represent single dives and filled triangles represent bout dives. Depths were combined, as were stationary and active single dives. Data are from four Steller sea lions, each of which performed 12 single dives and six dive bouts for a total of 72 trials.

not significantly greater than for single dives, even when time at the surface between dives was included. Calculating a 'recovery efficiency' ratio (as the volume of oxygen consumed divided by the cumulative recovery time) determined the amount of oxygen replenished per minute at the surface and showed a significant effect of dive type on recovery efficiency (LRT = 60.97, $P < 0.0001$). Recovery efficiency was the same for both single dive types (8.4 ± 1.6 ml O_2 kg^{-1} min^{-1}; $P = 0.060$), whereas bout dives had higher recovery efficiency than single dives (12.5 ± 2.1 ml O_2 kg^{-1} min^{-1}; $P < 0.0001$). This suggests that occasional surface intervals during dive bouts conveyed an advantage for gas exchange compared with single dives.

Dive components

Depth did not affect the DMR of separate dive components (LRT = 0.20, $P = 0.66$), so data from all depths were combined. However, oxygen consumption rates did differ between components (LRT = 11.44, $P = 0.0033$; Table 1). The transit portion of a dive had a significantly higher DMR than the bottom portion of a dive ($P < 0.01$). Activity level (stationary or active) during the bottom portion had no effect on DMR ($P = 1.0$), so data from stationary and active bottom portions could be combined (Fig. 3). The cost for transiting to and from depth was 20.5 ± 13.0 ml O_2 min^{-1} kg^{-1}, and the average cost for the bottom portion of a dive (regardless of activity) was calculated as 13.5 ± 4.1 ml O_2 min^{-1} kg^{-1}, and both were higher than metabolism at the surface (9.2 ± 1.6 ml O_2 min^{-1} kg^{-1}).

Validation

With the calculated costs of the separate dive components for transit, bottom and surface times, we were able to predict

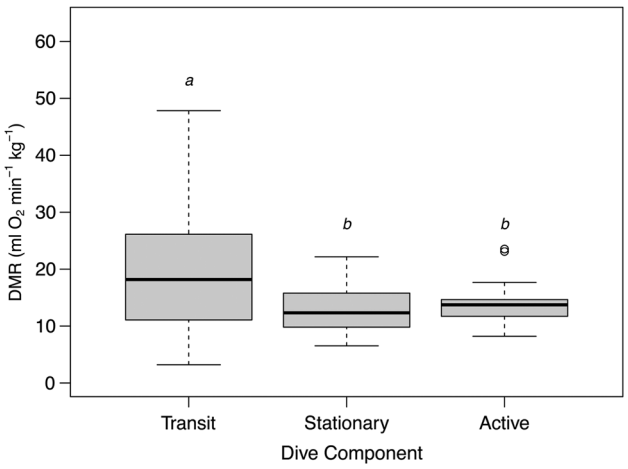

Figure 3: Diving metabolic rates (DMRs) of separate dive components calculated from the diving costs for Steller sea lions performing three dive types to 10 and 40 m. Dive types were as follows: transit dives with no bottom time; dives with 3 min of non-active bottom time; and dives with 3 min of active bottom time. Dive components include 'transit' (the cost of diving to and from depth), 'stationary' (the cost of being at depth with little to no activity) and 'active' (the cost of actively swimming at depth). Each box represents the calculated dive component for six dive trials from each of the four animals for a total of 24 trials for each dive component. Transit dives were significantly more costly than stationary or active components. Depths were combined because there was no statistical difference between 10 and 40 m.

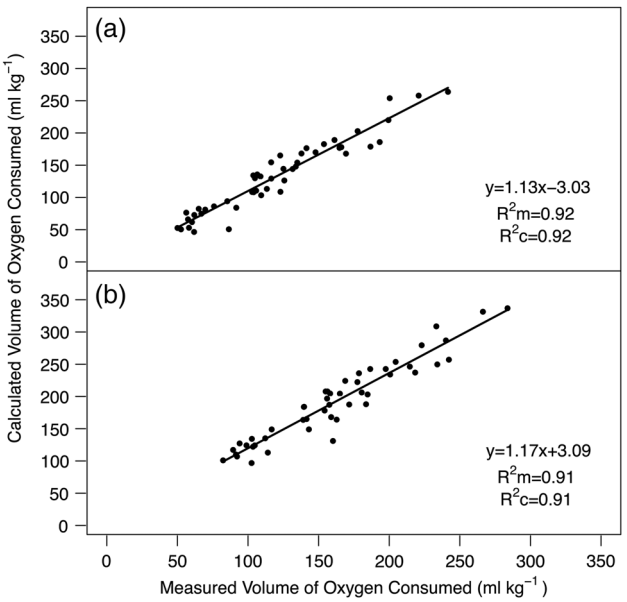

Figure 4: Volume of oxygen consumed by Steller sea lions during the submergence portion of dives (**a**) and the complete dive cycle (**b**) calculated from the estimated DMR of the transit, bottom and surface components of a dive as a function of the measured volume of oxygen consumption for the same dives. The submergence portion includes only the volume of oxygen consumed above resting metabolic rate during diving, whereas dive cycles include the volume of oxygen consumed during dives and at the surface. Each point represents a single dive bout. Data are from four Steller sea lions, each of which performed 12 dive bouts for a total of 48 trials. Equations are derived from linear mixed effects models. Marginal r^2 values (R^2m) are included for fixed effects and conditional r^2 values (R^2c) are included for random effects.

oxygen consumption for both 'dive only' (submergence time only; Fig. 4a) and complete 'dive cycles' (including all surface times; Fig. 4b) for a set of independent dive bouts from a previous study (Goundie *et al.*, 2015). There was a strong linear relationship between the calculated and measured volumes of oxygen consumed for the dive only portions (ANOVA, $F_{1,43} = 551.27$, $P < 0.0001$; slope = 1.13, $r^2 = 0.92$), with a slope that was significantly different from 1 [$P = 0.01$; 95% confidence interval (1.03, 1.23)]. On average, calculated oxygen consumption overestimated measured costs by ~5.9%. Comparing calculated and measured values for complete dive cycles also resulted in a strong linear relationship (ANOVA, $F_{1,43} = 453.47$, $P < 0.0001$; slope = 1.17, $r^2 = 0.91$). This also had a slope significantly different from 1 [$P = 0.004$; 95% confidence interval (1.07, 1.28)] and overestimated oxygen consumption by ~21.8%.

The difference (expressed as a percentage) between measured and calculated values for predictions of both dive only and the dive cycle was not affected by the volume of oxygen consumption or, by extension, the dive duration (dive only, ANOVA, $F_{1,43} = 0.53$, $P = 0.47$; and dive cycle, ANOVA, $F_{1,43} = 0.28$, $P = 0.60$).

Discussion

Foraging behaviour for diving animals is plastic, changing with the physiological capabilities of the animal and the conditions in which they hunt. Accurate activity-specific estimates of energy expenditure are needed to understand the costs and benefits associated with different foraging strategies. Our study quantified the costs of different portions of dives in Steller sea lions to estimate the costs of diving and evaluate the energetic consequences of changes in diving behaviour in response to environmental changes.

We found that transiting to and from depth was more costly than time spent at the bottom and that there were no differences in cost between the depths and activity levels we tested. This explained why longer single dives were less energetically expensive than multiple shorter dives. However, bouts of shorter dives were more time efficient, as oxygen was replenished more effectively when animals made multiple short dives. Our ability to predict total dive costs based upon individual dive components indicates that this may ultimately provide a useful tool to estimate diving costs of wild animals and to interpret aspects of foraging models and wild diving patterns.

Metabolic costs of dive components

As expected, the transiting portion of a dive was more costly than the bottom portion. This is likely to reflect a strategy of

increased transit speeds to attain depth quickly (Boyd *et al.*, 1995a). An increase in the number, speed or magnitude of flipper strokes has been shown to be directly related to higher costs of diving in other species (Williams *et al.*, 2004; Davis and Williams, 2012). Likewise, pinnipeds have also been observed to decrease swimming speeds and activity levels during the bottom portion of the dive to conserve energy (Crocker *et al.*, 2001; Hassrick *et al.*, 2007). This strategy trades the increased costs for attaining depth for the increased amount of time actively foraging, which is further maximized through reduced swimming speed at depth.

However, fast transit times and slow bottom times are not the only strategy for allocating time and energy that diving animals can employ to optimize foraging (Thompson *et al.*, 1993). An alternative strategy is for animals to conserve energy while transiting, either by slowing swimming speeds or by using passive gliding to get to and from depth (Williams *et al.*, 2000; Gallon *et al.*, 2007). These strategies maximize time spent foraging by minimizing oxygen consumption and thereby increasing overall aerobic dive time. Transit rates can be further increased for minimal extra cost by using changes in buoyancy to accelerate without increasing stroke rate (Hindell and Lea, 1998; Williams *et al.*, 2000; Crocker *et al.*, 2001; Davis *et al.*, 2001; Hassrick *et al.*, 2007). However, this behaviour is typically seen only with deep dives (>80 m) where changes in buoyancy are more pronounced (Williams *et al.*, 2000). Likewise, animals that exhibit reduced swimming speed on the transit portion of a dive (Gallon *et al.*, 2007) are generally those with longer aerobic dive limits (ADLs) that are also making long, deep dives.

As Steller sea lions are generally short, shallow divers (Merrick *et al.*, 1994; Merrick and Loughlin, 1997; Loughlin *et al.*, 1998) with short ADLs (Gerlinsky *et al.*, 2013), and our animals had maximal dive depths of 40 m, it is not surprising that they used the strategy of expending more energy to get to their foraging depth rapidly. This strategy has also been observed in another Otariid species, the Antarctic fur seal (Boyd *et al.*, 1995a). For shallow-diving animals with relatively short ADLs, the benefits gained by using reduced swimming speeds during transit (i.e. marginally increased ADL) would be less than the benefits associated with shorter transit times through increased swimming speed.

Surprisingly, the activity level during the bottom portion of dives (stationary vs. active) had no effect on DMR. This is probably because there was not enough difference between the two activity types in our study. Although sea lions remained fairly still at the single feeding tube for stationary bottom time trials, the animals periodically swam in tight circles around the tube to remain properly aligned with where the fish were delivered, possibly exaggerated by slight negative buoyancy at testing depths (Fahlman *et al.*, 2008a). This may have been energetically indistinguishable from the minimal efforts required to swim between the two tubes during active bottom time trials. There is evidence from wild pinnipeds to suggest that, although there is variation in swimming speed during the bottom portion of a dive when animals are actively foraging, there is little variation in the overall mean swimming speed (Hassrick *et al.*, 2007). This suggests that there would probably also be similar mean energetic costs between dives as well, which supports our finding of a single cost for both types of dives that had different types of activity.

Dive depth did not alter the cost of any dive component. We did not expect to see increased metabolic suppression in our study, as previous studies on diving Steller sea lions indicate that metabolism decreases only during longer dives (Hurley and Costa, 2001; Hastie *et al.*, 2006b; Hindle *et al.*, 2010) or for dives deeper than 50 m (Hastie *et al.*, 2006b). For our study, depth was limited at 40 m because the location of the dive set-up. Data on wild Steller sea lion dive patterns indicate that ~90% of dives are shallower than 50 m (Merrick and Loughlin, 1997), making the depths used in our study relevant to the majority of dives seen in the wild. Therefore, our estimates are most applicable to dives of similar durations to those used during our study.

Applications of results

One of the goals of our study was to determine whether the total cost of a dive could be estimated reasonably from a simple bioenergetic model of its component behaviours. Such a model would not only allow the energetic consequences of observed foraging behaviours to be quantified, but would also allow a retrospective analysis of a wealth of archived dive data to gain a better understanding of historical changes in foraging behaviour that may have occurred in response to past changes in the sea lion's environment.

Results of our validation demonstrated a very tight correlation between measured and calculated diving costs, both when calculated for only the submerged portion of the dive and for the complete dive cycles. The precision of our estimates was similarly high for both estimates. However, the accuracy of our estimates differed in that our model overestimated the total volume of oxygen consumed above resting levels during only the submerged time by 5.9%, but overestimated the costs for an entire dive cycle by 21.8%. This was unexpected given that most proxies for estimating oxygen consumption are more accurate when applied over an entire dive cycle (Fahlman *et al.*, 2008c; Young *et al.*, 2011), presumably because it represents a complete physiological event (Kooyman, 1985). The estimated error (average percentage residual of 9.5% for submergence only and 7.7% for dive cycles) was similar to the error seen when using other techniques to estimate oxygen consumption. For the same animals used in our study, there was a 7% error when using overall dynamic body acceleration to estimate oxygen consumption (Fahlman *et al.*, 2008c) and a 9–17% error when using heart rate to estimate oxygen consumption (Young *et al.*, 2011). However, it is important to note that different studies often calculate error in different ways such that direct comparisons should be made with caution.

The fact that our overestimates were higher when calculated over the entire dive cycle compared with submergence

time only suggests that the difference may lie in our estimates of surface metabolism. In our calculations, we used estimates of pre-dive surface metabolism (MR_S) to calculate both inter-dive and post-dive surface metabolism. The inter-dive and post-dive rates of oxygen consumption were assumed to be a simple additive component to the cost of diving, with no physiological interaction. If this assumption is incorrect, our estimates of metabolism during the inter-dive surface intervals and the post-dive recovery period could be inflated, and the effect would be greater for estimates calculated over the entire dive bout. Unfortunately, our data do not provide a means to separate and measure real surface costs between dives.

Despite the potential bias of surface costs, the correlation between the calculated and measured costs was very tight, indicating that our model has potential to be used to provide activity-specific estimates of energy expenditure for wild animals. The average overestimate remained constant across different dive types and durations, indicating that these overestimates could reasonably be used as a correction factor to improve accuracy when using this method to calculate the costs of submergence only or dive cycles of wild animals. Although there was variability in the individual differences between measured and calculated values, this would, in theory, average out with an increasing sample size and more dives. A parallel effort in improving this model would be to determine why we obtained overestimates with a goal to minimize this effect.

While our study reported a significant difference in the costs of transit and bottom time, the technique of applying separate costs to different components of the dive to estimate total costs is only warranted over the simpler technique of applying a constant cost estimate to all diving behaviour if it makes a difference to the end results. While the majority of dives performed by wild Steller sea lions are similar to those in our study, a significant portion is strikingly different. We can extrapolate the theoretical costs of different dives using the values from the present study. For example, the costs of completing 3 min dives to either 10 or 100 m (based upon our experimentally derived costs of transit and bottom time) would be 11% lower or 13% higher than those to 50 m, respectively. Therefore, for animals diving close to their aerobic dive limit regardless of depth, animals diving to a deeper depth would be at an energetic disadvantage owing to the greater proportion of time spent transiting, as well as less time to spend at the bottom foraging. These theoretical calculations suggest that differences or changes in dive behaviour have a significant cost, and provide justification that this technique is worth developing.

Of course, any application of this model to wild animals also assumes that the animals in our study behave in a similar manner to their wild counterparts while diving. To test this assumption, measures such as swim speed and flipper stroke rate should be compared between our animals and wild Steller sea lions to compare swimming effort between groups. Although we had no means of measuring swimming speed during the bottom portion of the dives in the present study, we were able to measure swimming speeds during the descent and ascent portions of the dives. Descent (1.68 ± 0.34 m s^{-1}) and ascent speeds (1.70 ± 0.35 m s^{-1}) were very consistent among all dives, regardless of depth or type. Surprisingly, we could find no published data on ascent and descent rates in wild Steller sea lions; however, the values we measured in the present study fell between speeds measured in other species of sea lions. New Zealand sea lions (*Phocarctos hookeri*) showed average descent speeds of 1.99 m s^{-1} and average ascent speeds of 1.97 m s^{-1} (Crocker *et al.*, 2001). Galapagos sea lions (*Zalophus wollabaeki*) had average descent speeds of 1.24 m s^{-1} and average ascent speeds of 1.26 m s^{-1} (Villegas-Amtmann *et al.*, 2008). These observations for other Otariid species also showed a consistency of speeds similar to what we observed, indicating that behaviour during descent and ascent is likely to be comparable between our animals and wild animals. Flipper stroke frequency was unfortunately not measured during the present study. However, as this provides an excellent estimate of effort, a future study comparing flipper stroke rate of the captive animals with wild animals would make an excellent addition and would help to test the validity of this model before applying it in the field.

Energetic consequences of dive strategies

The difference observed in the total costs of full dives was consistent with the results from the calculated costs of the separate dive components. Bouts of dives were more costly because of the larger proportion of time spent transiting, which was the portion of a dive with the highest metabolic cost. Hence, it is less energetically costly to make fewer longer dives than multiple shorter dives.

Although dive bouts had a higher rate of oxygen consumption than single dives, they did not have longer post-dive recovery times for similar total submergence times; in fact, it was marginally shorter than for single dives. This is partly because the sea lions were partly able to replenish oxygen stores during inter-dive surface intervals, as demonstrated by the relationship between cumulative surface time and total oxygen consumption. In fact, it appears that animals making multiple, shorter dives are able to replenish their oxygen more efficiently than animals making longer single dives because the rate of gas exchange would be greatest during the brief surface intervals when differences in partial pressures between the blood and the atmosphere are greatest (Kooyman *et al.*, 1973; Fahlman *et al.*, 2008b). This was confirmed by our measures of recovery efficiency, where bout dives indeed had higher efficiency than single dives.

As with most strategies, there are offsetting costs and benefits to both extended single dives and dive bouts with equal bottom times. The most obvious differences between single dives and dive bouts are in the comparisons of time and energetic cost. Our study confirmed that making multiple shorter dives (dive bouts) was more energetically costly than making equitable single dives. However, there is a benefit to using the dive bout strategy owing to its shorter total recovery time, which results in proportionally less time needed at the surface to replenish oxygen. Thus, while longer single dives appear to be a more efficient

use of energy, several shorter dives may be a more efficient use of time, because animals need to spend proportionally less time at the surface. Decreased time at the surface can not only increase chances of finding prey, but also possibly decrease vulnerability to predators (Heithaus and Frid, 2003).

Foraging models and wild dive patterns

The results from our study can be used to evaluate different models of diving strategies for foraging vertebrate divers. Various foraging models for breath-hold divers predict that animals should dive close to or slightly beyond their ADL (Kramer, 1988; Kooyman, 1989; Houston and Carbone, 1992; Carbone and Houston, 1996). This strategy maximizes foraging time without the added cost of using anaerobic metabolism. The near-complete depletion of oxygen stores also maximizes oxygen uptake at the surface owing to the large partial pressure difference between the animals' lungs and the air. The calculated ADL of Steller sea lions is ~3 min (calculated for the same animals used in the present study; Gerlinsky *et al*., 2013), which is similar to single dive times used in our study.

Our results, in combination with model predictions, suggest that the most efficient dive types should be multiple dives, close to the animals' ADL, with short surface intervals in between. This would minimize diving costs by keeping the proportion of time spent transiting as low as possible without using anaerobic metabolism, while allowing the greatest amount of time for foraging. Recovery efficiency would also be maximized with this diving strategy by having the greatest possible partial pressure difference at the beginning of each short surface interval.

Prey availability must also be considered when modelling optimal dive behaviour and interpreting dives in the wild. Foraging models of diving mammals suggest that animals should abandon a dive earlier when fewer prey are available (Thompson and Fedak, 2001). This would increase the cost of diving, because more time would be spent transiting; however, it would also provide the animal with more opportunity to look for prey in other locations.

Wild Steller sea lions show similar dive patterns to what our experimental results predict to be the most efficient strategy. Animals in the wild make multiple consecutive dives to depths of 20–50 m that are on average 1.9–2.4 min long (Merrick *et al*., 1994; Loughlin *et al*., 1998). Although these observed dive durations are below the animals' calculated ADL (Gerlinsky *et al*., 2013), it is unlikely that they are recovering fully between dives, which would effectively reduce the amount of time they could rely on aerobic metabolism alone for each subsequent dive.

Conclusions

Understanding the costs associated with foraging for Steller sea lions has become increasingly important to species management. As changes in prey are a potential factor contributing to their decline (Trites and Donnelly, 2003), it has become necessary to understand how foraging strategies, and the associated costs and benefits, may vary in response to these changes. Our results provide activity-specific estimates of diving costs to contribute to more accurate bioenergetic models for Steller sea lions as well as quantitative tests to help interpret foraging models and diving strategies better. This has possible applications for future studies on diving behaviour of wild animals, including the potential for historical analysis of archived dive data, and can help us to understand how shifts in prey are affecting overall energy balance, and therefore, the health of individuals in declining populations.

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